SILURIAN CRYPTOSPORES AND MIOSPORES FROM THE TYPE LLANDOVERY AREA, SOUTH-WEST WALES

by N. D. BURGESS

ABSTRACT. The oldest cryptospores and miospores have great significance in studies of the evolution of land plants: the former may represent the earliest direct evidence of such organisms and the latter may provide evidence for rhyniophytoid land plants as they have been recovered from the sporangia of *Cooksonia pertoni* Lang in the late Silurian. In the type Llandovery area, two distinct sporomorph assemblages are described from a composite section through uppermost Ordovician, Rhuddanian, Aeronian and basal Telychian strata. The older (latest Ordovician to late Aeronian) comprises eight genera and fourteen species of cryptospores (tetrads, pseudodyads, true dyads and monads). The younger (late Aeronian to Telychian) is dominated by smooth-walled trilete miospores of species of the genus *Ambitisporites*. Both assemblages have strong similarities to those described from similar horizons around the world. Specimens of *Ambitisporites dilutus* from the *sedgwickii* Graptolite Biozone of the Aeronian/Telychian type boundary section are the oldest known with unequivocal dating. They are used to define the base of the *Ambitisporites dilutus – A. avitus* Sporomorph Zone. Three new cryptospore genera (*Rimosotetras*, *Segestrespora* and *Velatitetras*) are erected and *Tetrahedraletes* is emended and synonomized with *Nodospora*. Six new cryptospore species (*Velatitetras laevigata*, *V. reticulata*, *V. rugulata*, *Rimosotetras problematica*, *Segestrespora laevigata* and *S. rugosa*), and two new varieties (*T. medenensis* vars *medenensis* and *parvus*) are described, and two combinations are made.

CURRENTLY sporomorphs provide the most convincing evidence for the existence of land plants in the late Ordovician and early Silurian (Gray 1985), the best being those with the greatest similarity to ones from living plants, or fossils of proven land-plants (Gray *et al.* 1982; Edwards *et al.* 1983; Gray 1985; Richardson 1985; Fanning *et al.* 1988). Spores in almost all such plants are produced in tetrads which separate on maturity to yield four trilete miospores. There are few records of trilete miospores in the Llandovery (Hoffmeister 1959; Cramer 1968, 1969; Pratt *et al.* 1978; Aldridge *et al.* 1979; Hill *et al.* 1985; Gray 1988; Richardson 1988). However, recent work has demonstrated the presence of permanently fused tetrads, dyads and monads, all of which can be enclosed within an envelope, in the late Ordovician and early Llandovery (e.g. Gray and Boucot 1971; Strother and Traverse 1979; Gray *et al.* 1982; Miller and Eames 1982; Gray 1985; Johnson 1985; Vavrdova 1982, 1984, 1988). As these unusually constructed cryptospores (*sensu* Richardson *et al.* 1984) may represent the oldest evidence of land-plants they have become important in the debate on the appearance and subsequent evolution of such organisms (Gray and Boucot 1977; Taylor 1982; Richardson 1985; Gray 1985, 1988).

Despite their importance, few assemblages of Ordovician and Llandovery sporomorphs have been described from well-dated sections, or ones covering a long stratigraphic interval (Pratt *et al.* 1978; Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985; Richardson 1988). This has hindered interpretation of the biostratigraphic and evolutionary significance of the sporomorphs. This paper presents full descriptions and stratigraphic ranges for those cryptospores and trilete miospores recovered from a composite section through the uppermost Ordovician and the majority of the Llandovery Series in the type Llandovery area (Cocks *et al.* 1984).

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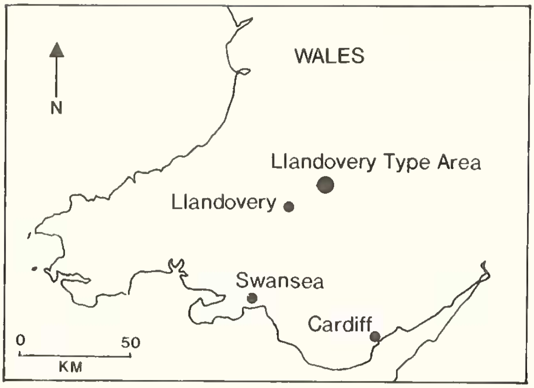
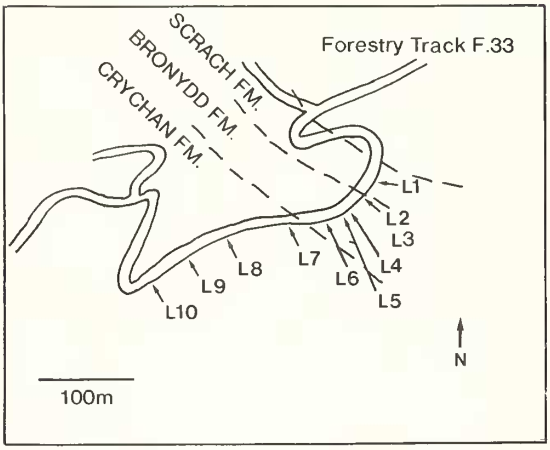
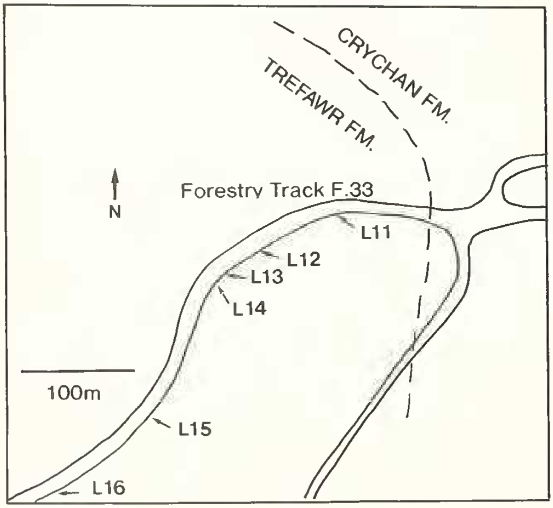


TEXT-FIG. 1. Location of the type Llandovery area in southern Wales.

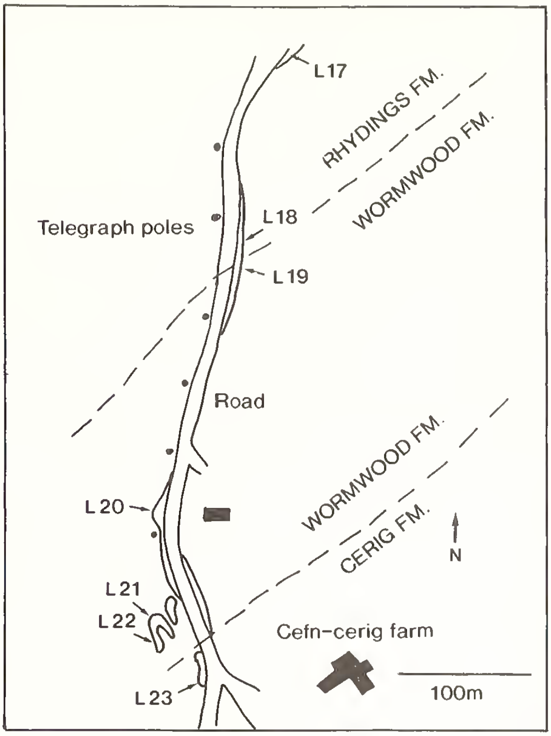


TEXT-FIG. 2. Locations of samples collected from the late Ordovician Scrach Formation to the early Llandovery Bronydd and Crychan formations in the type Llandovery area: Forestry track F.33, Crychan Forest near Llandovery (Ordnance survey map reference SO 84583964 at sample L1 = locality 24 of Cocks *et al.* 1984).



TEXT-FIG. 3. Locations of samples collected from the Rhuddanian/Aeronian type boundary section in the type Llandovery area: Forestry track F.33, Crychan Forest, near Llandovery (Ordnance survey map reference SO 83913960 at sample L11 = locality 38 of Cocks *et al.* 1984).

TEXT-FIG. 4. Locations of samples collected from the Aeronian/Teychian type boundary section in the type Llandovery area: roadside near Cefn Cerig farm, near Llandovery (Ordnance survey map reference SO 77543271 at sample L17 = locality 154 of Cocks *et al.* 1984).



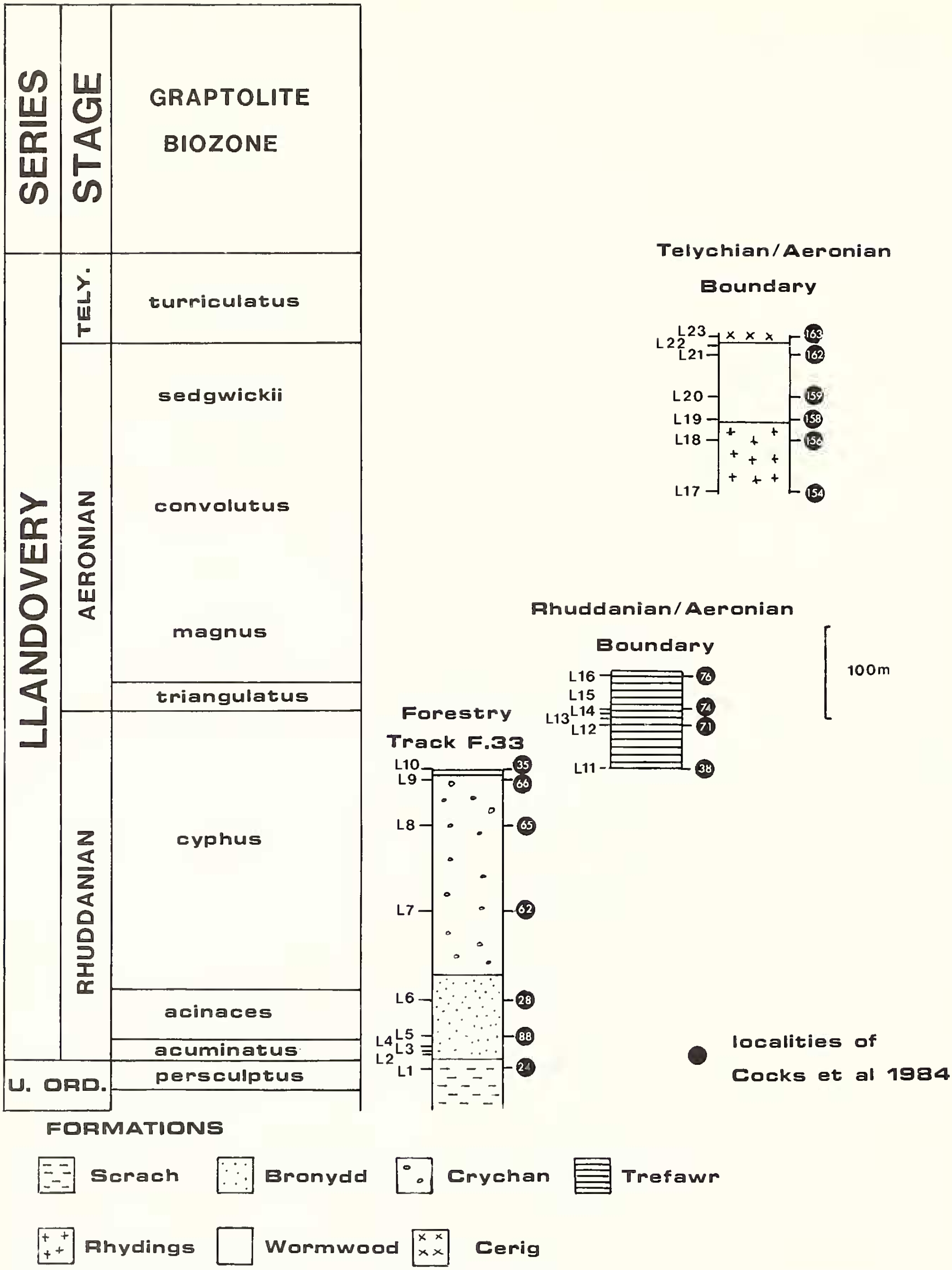
GEOLOGY, SAMPLING AND TECHNIQUE

The location of the type Llandovery area is presented in Text-figure 1. A single sample was collected from the uppermost Ordovician and twenty-two from the Llandovery Series. Sequences collected spanned the Ashgill/Rhuddanian boundary exposed along Forestry Track F. 33 next to the Afon Crychan river in Crychan Forest, c. 7 km north-east of Llandovery (Text-fig. 2), the Rhuddanian/Aeronian type boundary section (Text-fig. 3) and the Aeronian/Telychian type boundary section (Text-fig. 4) (Cocks *et al.* 1984). The top *c.* 100 m of the sequence in the type area were not sampled: this interval covers the *crispus* to *crenulatus* Graptolite Biozones. The stratigraphical framework of the samples is given in Text-figure 5.

The Llandovery sediments of the type area were deposited during a transgression which affected the whole of the Anglo-Welsh Basin (Cocks *et al.* 1984; Ziegler *et al.* 1968). As a consequence the samples collected during this study are from increasingly distal marine facies further up the section (Table 1). However, there may be slight shallowing event in the Wormwood Formation.

TABLE 1. Distribution of samples by geological formation with the ages and probable depositional environment.

Samples	Formation	Age	Probable depositional environment (Cocks *et al.* 1984)
L23	Cerig	early Telychian	Open marine shelf
L19–L22	Wormwood	late Aeronian	Open marine shelf
L17–L18	Rhydings	late Aeronian	Open marine shelf
L11–L16	Trefawr	early Aeronian	Open marine shelf
L7–L10	Crychan	late Rhuddanian	Open marine prograding delta lobe
L2–L6	Bronydd	early Rhuddanian	Mud-dominated marine shelf with storms
L1	Scrach	latest Ashgill	Shallow sub-tidal or even intertidal



TEXT-FIG. 5. Biostratigraphic and lithostratigraphic position of samples from the type Llandovery area, in relation to localities of Cocks *et al.* (1984).

Samples varied from dark mudstones in the Scrach and Bronydd formations through to muddy siltstones and silty mudstones for the remainder of the sequence. Palynomorphs were extracted using standard palynological methods (HCl then HF acids followed by sieving with 10 μm filter mesh and separation of the organic fraction using zinc bromide solution (S.G. 2·0)). Residues were oxidized in cold Schultze's solution for c. 48 hours. The sporomorphs remain dark, but poor preservation did not allow any further extension of the oxidation time. When this was attempted all the sporomorphs disintegrated. After oxidation, the acidic residues were neutralized with distilled water.

For light microscope observation, measured volumes of material were strewed on to glass coverslips, dried, and the coverslips attached to glass slides with 'Elvacite' plastic mounting medium.

Photomicrographs were taken on FP4 film using a Zeiss photomicroscope III (no. 2562) housed in the Palynology Laboratory of the British Museum (Natural History) (BM(NH)), and using Nomarski differential interference contrast with an orange filter to reduce contrast between the palynomorphs and the background.

SYSTEMATIC PALAEONTOLOGY

Preamble. Sporomorphs are described, where possible, using the standard terminology of Grebe (1971). Specimen dimensions are presented as the minimum and maximum of the range, with the mean in brackets. Stratigraphic range refers to range within the type Llandovery area only. The stratigraphical occurrence of taxa is shown in Text-figure 7 and the stratigraphical distribution and correlation of the samples in Text-figure 5.

Specimens are located by means of standard England Finder and microscope stage co-ordinates taken from the Zeiss photomicroscope III (no. 2562) housed in the Palynology Laboratory at the BM(NH). All figured specimens are also ringed with a red indelible pen. Slides and stubs containing figured specimens (prefixed FM) are stored in the Palynology collection at the BM(NH).

Anteturma CRYPTOSPORITES Richardson *et al.*, 1984

1. *Cryptospore tetrads*

This group comprises tetrads and dyads which are not found separated into individual components spores and which are believed to be 'permanently' fused. They may also be enclosed within a sculptured or non-sculptured envelope.

Genus TETRAHEDRALETES Strother and Traverse, 1979 emend.

Type species. *Tetrahedraletes medinensis* Strother and Traverse, 1979 from the Tuscarora Formation, Pennsylvania, USA.

Emended diagnosis. Permanent tetrahedral cryptospore tetrads, permanently fused. Tetrads sub-circular to circular in outline and composed of four laevigate, crassitate, sub-triangular 'spores'. Crassitudes of individual 'spores' $\pm$equatorial, fused or discrete. Distal 'spore' walls tend to invaginate, but can remain inflated.

Discussion. *Tetrahedraletes* Strother and Traverse was erected to encompass 'tetrads of inaperturate, sub-triangular spores or spore-like palynomorphs arranged in tightly adhering tetrahedron configuration, with the spore walls collapsed towards the centre' (Strother and Traverse 1979, p. 8). *Nodospora*, a similar genus, was defined for 'tetrads of inaperturate spores or spore-like palynomorphs, spherical to sub-spherical in outline, which are arranged in a cross configuration' Strother and Traverse (1979, p. 10). Data collected here and in other recent publications (e.g. Gray *et al.* 1985; 1986; Gray 1985; 1988) indicate that the type specimens of *Tetrahedraletes* (*T. medinensis*) and *Nodospora* (*N. burnhamensis*) should be placed in synonomy, the two taxa representing different compressional morphologies of otherwise identical tetrads. Hence, in this publication all such tetrads are placed in *Tetrahedraletes* and the diagnosis of this genus emended accordingly.

Tetrahedraletes medinensis Strother and Traverse, 1979 emend.

This species has been subdivided into two varieties based on size because the original specimens (Strother and Traverse 1979) are much larger than those recorded from the late Ordovician and early Llandovery (e.g. Gray 1988).

Tetrahedraletes medinensis Strother and Traverse, 1979 var. *medinensis* var. nov.

Holotype and type locality. Strother and Traverse, 1979, pl. 1, fig. 5: Harvard Paleobotanical Collections no. 60289, slide no. 75-4/A3, location on slide 34·8 mm × 107·9 mm, reference point 13·3 mm × 109·2 mm. Samples 75-4, Tuscarora Formation; Section – Mann Narrows along route 322, north-west of Burnham, Mifflin County, Pennsylvania, USA.

Description. As for Strother and Traverse (1979).

Comparison. Cryptospores of *Tetrahedraletes medinensis* var. *parvus* var. nov. are < 35 μm in diameter, but otherwise identical.

Remarks. This variety of *T. medenensis* is common in the basal Wenlock (Burgess and Richardson 1991) but is not known from the uppermost Ordovician or early Llandovery of the type area where the following variety is found (also see Gray 1988).

Tetrahedraletes medinensis var. *parvus* var. nov.

Plate 1, figs 1–4

1985 *Tetrahedraletes* cf. *T. medinensis* Gray, fig. 5 F–H.

EXPLANATION OF PLATE 1

All figures × 1000 unless stated otherwise.

Figs 1–4. *Tetrahedraletes medinensis* Strother and Traverse, 1979 emend. var. *parvus* var. nov. 1, FM 187, holotype (slide Llan 8B/12, 178 1170; E.F. no: S47/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, × 2000. 2, FM 188 (slide Llan 8B/8, 061 1283; E.F. no: F58/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 3, FM 92 (slide Llan 5/2, 130 960; E.F. no: N26/1), sample L16, Trefawr Formation, *triangulatus* Graptolite Biozone. 4, FM 189 (slide Llan 1/1, 112 1204; E.F. no: K50/4), sample L11, Trefawr Formation, *cyphus* Graptolite Biozone.

Figs 5 and 6. *Velatitetras laevigata* gen. et sp. nov. 5, FM 190 (slide Llan 8B/11, 179 1294; E.F. no: S59/S60), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 6, FM 191, holotype (slide Llan 2/1, 050 1215; E.F. no: E51/4, sample L12, Trefawr Formation, *cyphus* Graptolite Biozone.

Figs 7–9. *Velatitetras reticulata* gen. et sp. nov. 7, FM 91 (slide Llan 1/2, 232 1110: E.F. no: Y41/2), sample L11, Trefawr Formation, *cyphus* Graptolite Biozone. 8, FM 197 holotype (slide Llan 8B/9, 128 1253: E.F. no: N55/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 9, FM 192 (slide Llan 8B/8, 106 1304; E.F. no: K60/61/L60/61), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

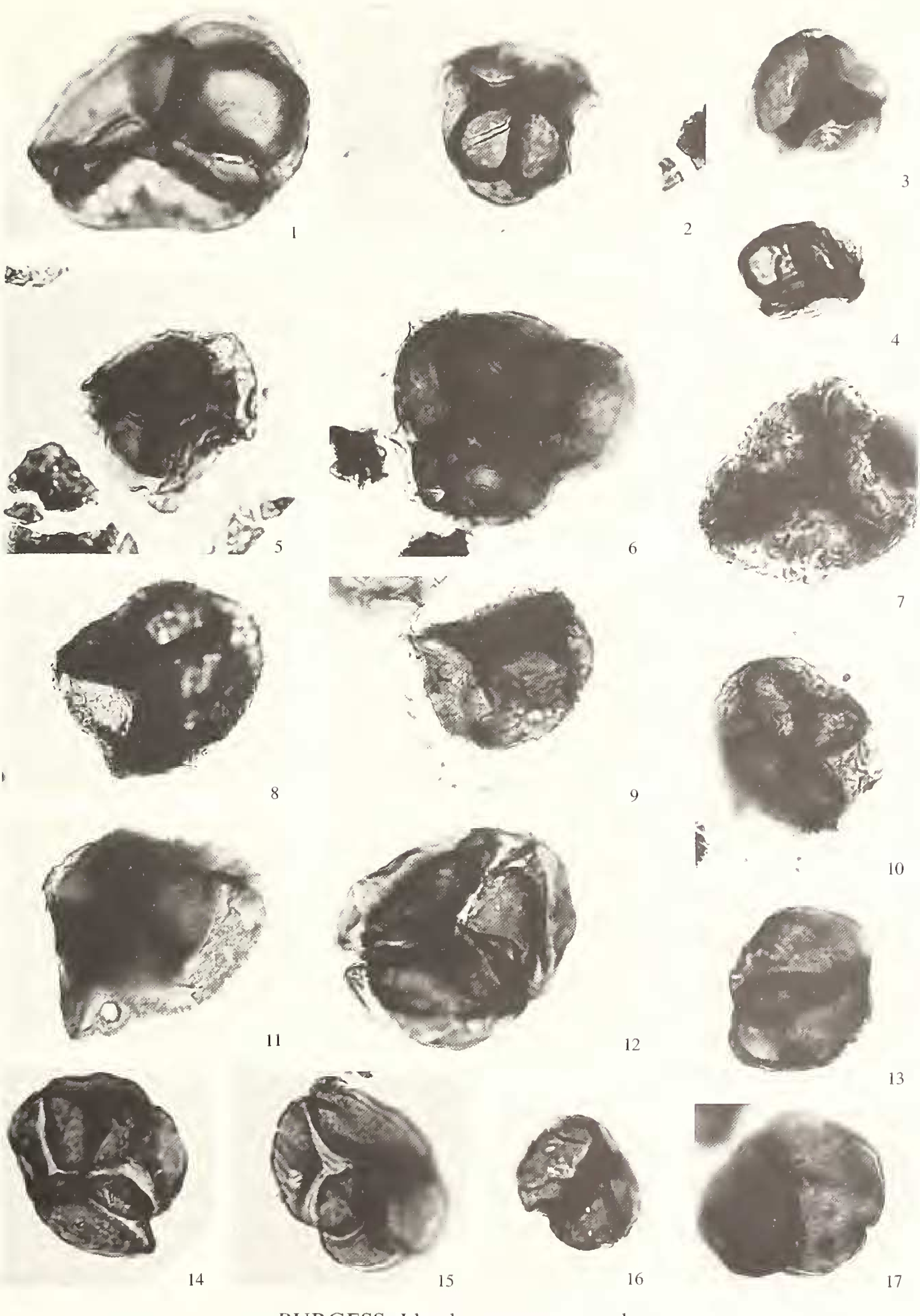
Fig. 10. *Velatitetras rugulata* gen. et sp. nov. FM 194, holotype (slide Llan 8B/12, 128 1220; E.F. no: M52/3/M51/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 11. *Velatitetras* sp. A. FM 195 (slide Llan 8B/15, 118 1277; E.F. no: M58/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Figs 12, 14, 15. *Rimosotetras problematica* gen. et sp. nov. 12, FM 196 (slide Llan 8B/12, 240 1080; E.F. no: Y38/3), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 14, FM 198, holotype (slide Llan 8B/6, 138 1228; E.F. no: 053/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 15, FM 199 (slide Llan 8B/8, 147 1089; E.F. no: P38/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Figs 13, 16, 17. *Pseudodyadospora* cf. *laevigata* Johnson, 1985. 13, FM 197 (slide Llan 8B/26, 035 1250; E.F. no: C55/1/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 16, FM 200 (slide Llan 8B/22, 226 1112; E.F. no: X41/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 17, FM 201 (slide Llan 8B/12, 240 1095; E.F. no: Y39/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

PLATE 1



BURGESS, Llandovery sporomorphs

1985 *Tetrahedraletes* cf. *T. medinensis* Gray *et al.*, p. 524, fig. 5 F–H.
1986 *Tetrahedraletes* cf. *T. medinensis* Gray *et al.*, p. 451, fig. 7, items 1–7.
1988 'Smooth walled tetrads', Gray, p. 355, pl. 1, figs 1 and 5.
1988 *Tetrahedraletes* sp., Richardson, pl. 19, fig. 1.

Holotype and type locality. FM 187, Pl. 1, fig. 1, slide Llan 8B/12, 178 1170, E.F. no: S47/1, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

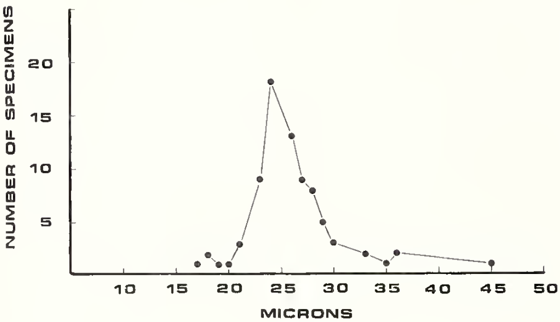
Paratypes. FM 188, Pl. 1, fig. 2, slide Llan 8B/8, 061 1283, samples L5; Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone; FM92, Pl. 1, fig. 3, slide Llan 5/2, 130 0960, sample L20, Aeronian/Telychian boundary section, Wormwood Formation, *sedgwickii* Graptolite Biozone; FM 189, Pl. 1, fig. 4, slide Llan 1/1, 020 1204, sample L11, Rhuddanian/Aeronian boundary section, Trefawr Formation, *cyphus* Graptolite Biozone.

Derivation of name. Latin *parvus*, small.

Diagnosis. A variety of *Tetrahedraletes medinensis* < 35 μm in diameter with low, narrow, rounded and unfused equatorial crassitudes.

Description. Laevigate obligate tetrads, sub-circular to circular in outline and preserved in a variety of compressional morphologies depending on the degree of rotation of the tetrad from an apical view prior to compression. Individual 'spores' laevigate, amb sub-circular to sub-triangular, joined by unfused equatorial crassitudes 1–5 μm wide. Proximal surface not observed. Distal exine 1–2 μm thick and invaginated in most specimens.

Dimensions. Tetrads 19 (26) 30 μm in diameter (150 specimens measured, see Text-figure 6 for range of measurements).



TEXT-FIG. 6. Size frequency distribution of a hundred *Tetrahedraletes medinensis* var. *parvus* tetrads from sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Biostratigraphical range. Latest Ordovician (*persculptus* Graptolite Biozone), to early Telychian (*turriculatus* Graptolite Biozone; Text-fig. 7).

Comparisons. Tetrahedraletes medinensis var. *medinensis* is larger (> 35 μm). Specimens described as *Tetrahedraletes* cf. *T. medinensis* (Gray 1988) from various sections spanning the Ordovician/Silurian boundary around the world have essentially identical measurements to those described above.

Remarks. Gray (1988) has presented data showing that tetrads gradually increase in size over the Ordovician/Silurian boundary and states that this increase continues through the Llandovery. In the Anglo-Welsh Basin, *T. medinensis* var. *parvus* var. nov. is the dominant variety in the latest Ordovician and early Llandovery, whereas *T. medinensis* var. *medinensis* Strother and Traverse, 1979 dominates in the basal Wenlock (Burgess and Richardson 1991).

Genus VELATITETRAS gen. nov.

Type species. Velatitetras laevigata sp. nov.

This genus is erected to accommodate tightly adherent cryptospore tetrads enclosed within an envelope. Some specimens of *Nodospora* Strother and Traverse are believed to possess an envelope (e.g. *N. retimembrana*). However, because the type species of *Nodospora* (*N. burnhamensis*) lacks an envelope and is considered synonomous with the type species of *Tetrahedraletes* (*T. medinensis*) the genus *Nodospora* cannot be used for enveloped forms. *Steganbiquadrella* Johnson was erected for palynomorphs with four loosely-attached inaperturate vesicles enclosed within an envelope. This genus cannot be used to accommodate tightly-adherent tetrahedral tetrads enclosed within an envelope.

Derivation of name. Latin *velatus*, covered; *tetras*, tetrad.

Diagnosis. Obligate cryptospore tetrads composed of tightly-adherant laevigate sub-triangular to sub-circular 'spores' with low and rounded ±fused equatorial crassitudes. Tetrads enclosed within a closely adherent to completely separated, ±ornamented envelope; when envelope tightly-adpressed any ornamentation passes over 'spore' contacts uninterrupted.

Velatitetras laevigata sp. nov.

Plate 1, figs 5 and 6

1985 'Obligate tetrad with smooth perispore', Gray, p. 177, pl. 1, figs 2 and 3.
1988 'Spore tetrad with smooth or possibly degraded reticulate envelope', Gray, p. 355, pl. 1, fig. 3.
1988 *Nodospora* sp. B, Richardson, p. 94.

Holotype and type locality. FM 191, Pl. 1, fig. 6, slide Llan 2/1, 050 1215, E.F. no: E51.4, sample L12 (Text-fig. 3), Rhuddanian/Aeronian type boundary section, Trefawr Formation, *cyphus* Graptolite Biozone, late Rhuddanian.

Paratype. FM 190, Pl. 1, fig. 5, slide Llan 8B/11, 179 1294, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *laevigatus*, smooth.

Diagnosis. A *Velatitetras* with cryptospore tetrad enclosed within a thin, laevigate and often folded envelope.

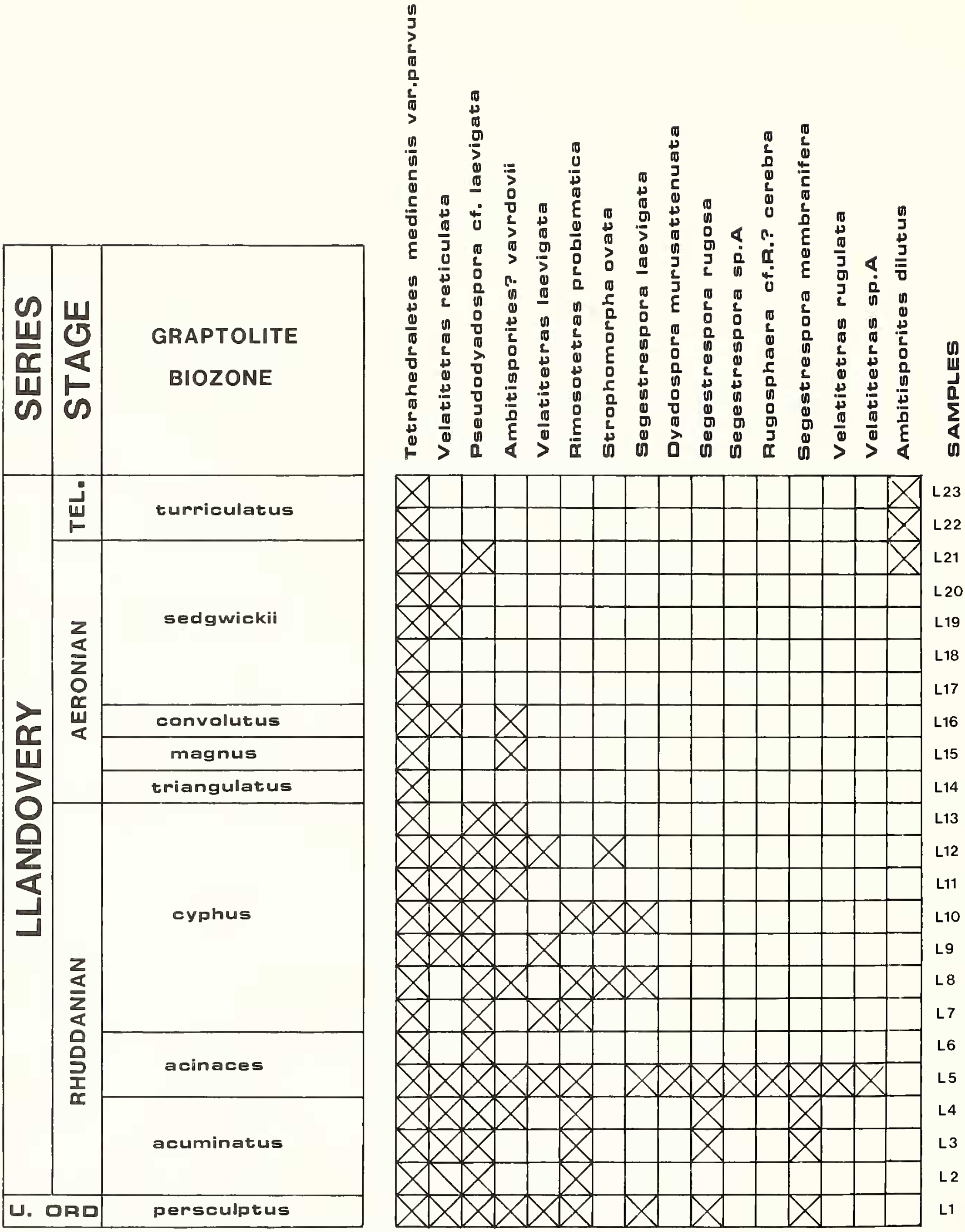
Description. Obligate tetrads, sub-circular to circular in outline, totally enclosed within an envelope. Tetrads composed of laevigate, sub-triangular 'spores' with unfused, low and rounded equatorial crassitudes 1–3 μm wide; distal polar exine *c.* 1 μm thick. Envelope laevigate, diaphanous, folded and < 1 μm thick; varies from completely separated, to closely adpressed to tetrad.

Dimensions. Enclosed tetrads 21 (27) 34 μm in diameter (22 specimens measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone), to late Rhuddanian (*cyphus* Graptolite Biozone; Text-fig. 7).

Comparisons. Gray (1985, pl. 1, figs 2 and 3; 1988, pl. 1, fig. 3), illustrated small (c. 25 μm) and essentially identical tetrads enclosed within smooth envelopes from the Late Ordovician of America.

TEXT-FIG. 7. Biostratigraphic and lithostratigraphic ranges of sporomorphs from the type Llandovery area. Note that the majority of the Telychian was not sampled.



TEXT-FIG. 7. Biostratigraphic and lithostratigraphic ranges of sporomorphs from the type Llandovery area. Note that the majority of the Telychian was not sampled.

Velatitetras reticulata sp. nov.

Plate 1, figs 7–9.

1985 Obligate tetrad with 'reticulate perispore', Gray, p. 177, pl. 1, figs 4–9; pl. 2, fig. 17.
1988 Obligate tetrad with 'reticulate envelope', Gray, p. 355, pl. 1, figs 2, 4, 6.

Holotype and type locality. FM 192. Pl. 1, fig. 8, slide Llan 8B/9, 128 1253, E.F. no: N55/2, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Paratypes. FM 91, Pl. 1, fig. 7, slide Llan 1/2, 232 1110, sample L11, Rhuddanian/Aeronian boundary section, Trefawr Formation, *cyphus* Graptolite Biozone; FM 193, Pl. 1, fig. 9, slide Llan 8B/8, 106 1304, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *reticulatus*, netted, marked with a network – refers to arrangement of muri on envelope.

Diagnosis. A *Velatitetras* with cryptospore tetrad enclosed within an envelope ornamented with muri forming a reticulum with small lumen.

Description. Obligate tetrads sub-circular to circular in outline, totally enclosed within an envelope. Tetrads composed of laevigate, inaperturate, sub-triangular to sub-circular 'spores' with unfused equatorial crassitudes 1–3 μm wide; exine at distal pole *c*. 1 μm thick. Envelope closely adpressed to widely separated from enclosed tetrad and ornamented with low (*c*. 1 μm), rounded muri 0·5 (1) 1·5 μm wide, which usually form an ill defined reticulum 1–3·5 μm in maximum diameter, although this may be of regular size and distribution over the envelope.

Dimensions. Enclosed tetrads 22 (27) 35 μm in diameter (14 specimens measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to late Aeronian (*sedgwickii* Graptolite Biozone; Text-fig. 7).

Comparisons. Comparable specimens have been described by Gray (1985, pl. 1, figs 4–9; pl. 2, fig. 17) and Gray (1988, pl. 1, figs 2, 4, 6) from the Ashgill of the USA. *Velatitetras rugulata* sp. nov. is of similar size, but has sinuous rugulae on its envelope. '*Nodospora*' *retimembrana* Miller and Eames, 1982 is much larger (34–60 μm) and the reticulum on the envelope is both larger and more regularly arranged.

Velatitetras rugulata sp. nov.

Plate 1, fig. 10

Holotype and type locality. FM 194, Pl. 1, fig. 10, slide Llan 8B/12, 128 1220, E.F. no: M52/3/M51/4, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Derivation of name. Latin *rugulatus*, refers to rugose ornamentation on envelope.

Diagnosis. A *Velatitetras* with cryptospore tetrad enclosed within an envelope ornamented with sinuous to convolute and anastomosing rugulae.

Description. Obligate tetrads sub-circular to circular in outline, totally enclosed within an envelope. Tetrad composed of laevigate, inaperturate, sub-triangular 'spores' with low and rounded unfused equatorial crassitudes 1–3 μm wide; exine at distal pole *c*. 1 μm thick. Envelope closely adpressed to completely separated from enclosed tetrad and ornamented with low, rounded rugulae 0·5–1 μm wide, < 1 μm high and 1·5 (2·5) 3 μm apart; rugulae are closely spaced, slightly sinuous to convolute and occasionally anastomosing.

Dimensions. Enclosed tetrads 24 (28·5) 33 μm in diameter (13 specimens measured).

Biostratigraphic range. Early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. Velatitetras reticulata sp. nov. is of similar size but the muri on its envelope form a reticulum. '*Nodospora*' *rugosa* Strother and Traverse, 1979, *Nodospora* sp. A Richardson 1988, and *N.* cf. *rugosa* Miller and Eames 1982 are much larger (> 43 μm).

Velatitetras sp. A

Plate 1, fig. 11

?1988 *Nodospora* sp. E, Richardson, p. 94.

Figured specimen. FM 195, Pl. 1, fig. 11, slide Llan 8B/15, 118 1277, E.F. no: M58/1, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Description. Obligate tetrad sub-circular in outline, totally enclosed within an envelope. Tetrad composed of laevigate, inaperturate, sub-triangular 'spores' with low and rounded crassitudes 1–3 μm wide. Envelope separated from tetrad and ornamented with closely packed grana.

Dimensions. 1 specimen with enclosed tetrad of 25 μm diameter.

Biostratigraphic range. Bronydd Formation, *acinaces* Graptolite Biozone (Text-fig. 7).

Comparisons. The granulate ornament on the envelope separates this tetrad from all other specimens. *Segestrespora* sp. A has a similarly ornamented envelope surrounding a pseudodyad.

Genus RIMOSOTETRAS gen. nov.

Type species. Rimosotetras problematica sp. nov.

Derivation of name. Latin *rimosus*, cracked.

Diagnosis. Adherent, but usually partially separating, tetrahedral tetrads composed of alete, laevigate, sub-triangular to circular, ±crassitate spores or spore-like units.

Remarks. In *Tetrahedraletes* Strother and Traverse, 1979 emend. the spores comprising the tetrad are much more tightly adherent. Tetrads of *Ambitisporites* Hoffmeister, 1959 separate more readily and produce miospores with obvious trilete marks.

Rimosotetras problematica sp. nov.

Plate 1, figs 12, 14, 15

1971 'Spore tetrad', Gray and Boucot, fig. 1(g).
1985 'Loose tetrads', Richardson, p. 29, pl. 15, figs 5 and 6.
1988 *Nodospora burnhamensis* 'loose tetrad', Richardson, pl. 19, figs 11 and 12.

Holotype and type locality. FM 198, Pl. 1, fig. 14, slide Llan 8B/6, 138 1228, E.F. no: 053/1, sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone, Rhuddanian.

Paratypes. FM 196, Pl 1, fig. 12, slide Llan 8B/12, 240 1080; FM 199, Pl. 1, fig. 15, slide Llan 8B/8, 147 1089, both sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *problematicus*, problematic; refers to problematic nature of these sporomorphs which are similar to permanently fused cryptospore tetrads, but which appear to separate into alete 'spores', in other ways similar to trilete miospores.

Diagnosis. A *Rimosotetras* with sub-triangular 'spores' possessing rounded, non-projecting, equatorial crassitudes.

Description. Cryptospore tetrads sub-circular to circular in outline and preserved in a variety of compressional morphologies reflecting rotation of tetrad from an apical view prior to compression. Tetrads composed of loosely attached, frequently partially separated, laevigate, alete or indistinctly trilete, sub-triangular to sub-circular 'spores' with narrow and rounded equatorial crassitudes 0·75 (1·5) 2·5 μm wide. Distal exine convex *c*. 1 μm thick, usually inflated, but can be invaginated. Proximal surface lacks sutures typical of trilete miospores, although specimens may have a crack or split at the position of a trilete mark indicating a weakness of the exine.

Dimensions. Tetrads 23 (28) 42 μm in diameter (38 specimens measured). Individual spores 15 (22) 35 μm in diameter (67 measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to late Rhuddanian (*cyphus* Graptolite Biozone) (Text-fig. 7).

Comparisons. Comparable 'loose' tetrads have been recorded in the Rhuddanian of Libya by Richardson (in Hill *et al*. 1985, p. 29) and Richardson (1988). The spore tetrad from North America drawn by Gray and Boucot (1971, fig. 1(g)) also appears similar.

2. *Cryptospore dyads*

This group encompasses permanently fused dyads (pseudodyads) which may be enclosed within a variously ornamented envelope and dyads which readily separate into two alete spores (true dyads).

Genus PSEUDODYADOSPORA Johnson, 1985

Type species. *Pseudodyadospora laevigata* Johnson, 1985.

Pseudodyadospora cf. *laevigata* Johnson, 1985

Plate 1, figs 13, 16, 17

Figured specimens. FM 197, Pl. 1, fig. 13, slide Llan 8B/26, 035 1250; FM 200, Pl. 1, fig. 16, slide Llan 8B/22, 226 1112; FM 201, Pl. 1, fig. 17, slide Llan 8B/12, 240 1095, all specimens sample L5 (Text-fig. 2), Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Description. Pseudodyads elliptical to sub-circular or rarely circular in outline. 'Spores' of pseudodyad joined by a single encircling darkened band 1 (2) 3 μm wide providing no evidence for 'spore' separation. 'Spores' are of unequal size in 62% of the specimens, laevigate, and usually distally convex, although they can be invaginated. Exine often folded and 0·5–1 μm thick at distal pole.

Dimensions. Pseudodyads 22 (26) 42 μm long and 16 (22) 28 μm wide at equator (50 specimens measured). Length to width ratio = 1·3.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to late Aeronian (*sedgwickii* Graptolite Biozone; Text-fig. 7).

Comparisons. *Pseudodyadospora laevigata* Johnson, 1985 is similar in outline, the variable size of the 'spores' and the fused suture between the 'spores', but is somewhat larger (41 (52) 60 μm long), although there is some overlap in the sizes. Dyads in *Segestrespora* gen. nov. possess an envelope surrounding an otherwise similar pseudodyad. Dyads of the genus *Dyadospora* Strother and Traverse, 1979 have well developed lines of separation between the equally sized spores, and are generally seen partially separated into two alete sporomorphs (Burgess and Richardson 1991).

Genus SEGESTRESPORA gen. nov.

Type species. Segestrespora (*Dyadospora*) *membranifera* (Johnson) comb. nov.

Derivation of name. Latin *segestre*, covering or wrapper.

Diagnosis. Bipolar, laevigate and permanently fused pseudodyads, divided by a single central to slightly off-centred thickened encircling band, and totally enclosed within a closely adherent to completely separated envelope which either lacks ornamentation, or has apiculi, muri, rugulae or verrucae.

Remarks. In some specimens an envelope can not be easily seen. However, if any sculpture passes over the 'spore' contact uninterrupted, then an envelope is assumed to be present and specimens are assigned to *Segestrespora*.

Comparisons. The genus *Pseudodyadospora* Johnson is for obligate pseudodyads with only one wall-layer, which can be sculptured. In *Dyadospora* Strother and Traverse, the dyads lack an envelope and are readily separated into two laevigate alete spores.

Segestrespora (*Dyadospora*) *membranifera* (Johnson, 1985) comb. nov.

Plate 2, figs 2–5

1985 *Dyadospora membranifera* Johnson [*partim*], p. 336, pl. 7, figs 1–3, 5, 6, *non* pl. 7, fig. 7.
1988 *Pseudodyadospora* cf. *Dyadospora membranifera*, Richardson, p. 94, pl. 15, figs 1 and 2.

Holotype and type locality. Johnson, 1985, pl. 7, figs 1–3: sample TMH81-11-26, location EF D35–4; c. 75 m from base of Mill Hall section, Tuscarora Formation. Section – 200 m long and located 250 m above US Route 220, 1 km SE of Mill Hall, Clinton County, Pennsylvania, USA.

Figured specimens. FM 203, Pl. 2, fig. 2, slide Llan 8B/7, 198 1020; FM 204, Pl. 2, fig. 3, slide Llan 8B/7, 220 2100; FM 205, Pl. 2, fig. 3, slide Llan 8B/11, 240 1170; FM 206, Pl. 2, fig. 5, slide Llan 8B/10, 130 1150, all sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Diagnosis. A *Segestrespora* where the envelope is ornamented with narrow muri which form a low, regular to irregularly sized and shaped reticulum.

Description. Pseudodyads elliptical to sub-circular in lateral view and totally enclosed within an envelope. Individual 'spores' of pseudodyad convex in lateral compression. Exine *c.* 1 μm thick with rare folds. A single darkened, possibly thickened, encircling band 1–2 μm wide joins the 'spores' which are anisomorphic in *c.* 75% of the specimens. The envelope is diaphanous and may be tightly adherent to the pseudodyad and difficult to resolve, or completely separated. Envelope is ornamented with muri, 0·5–1 μm wide and *c.* 0·5 μm high, which form a regularly to irregularly sized and shaped reticulum with lumen 1·5 (2) 3 μm in diameter.

Dimensions. Pseudodyads 25 (29) 31 μm long, 18 (20) 22 μm wide at equator (12 specimens). Length to width ratio = 1·4.

Biostratigraphic range. Late Ordovician (*persculptus* Graptolite Biozone) to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. Those specimens of '*Dyadospora membranifera*' Johnson, 1985 which possessed a reticulate envelope are members of this species, but those with a laevigate envelope are transferred to another species (see below). Specimens referred to *Pseudodyadospora* cf. *Dyadospora membranifera* by Richardson, 1988 are also members of this species. When specimens of *Segestrespora membranifera* have lost their membrane they are placed in *Pseudodyadospora laevigata* Johnson, 1985.

Segestrespora laevigata sp. nov.

Plate 2, fig. 1

?1982 *Dyadospora murusdensa* with 'membrane', Miller and Eames, p. 248.
1985 '*Dyadospora membranifera*' Johnson, [*partim*], p. 336, pl. 7, fig. 7, *non* pl. 7, figs 1–3, 5, 6.
?1985 *Dyadospora murusdensa* 'with diaphanous sheath', Richardson in Hill *et al.*, p. 29.

Holotype. Johnson, 1985, pl. 7, fig. 7, Sample TMH81-8, c. 125 m above the base of the Mill Hall section, Tuscarora Formation. Section – 200 m long and located 250 m about US Route 220, 1 km SE of Mill Hall, Clinton County, Pennsylvania, USA.

Figured specimen. FM 202, Pl. 2, fig. 1, slide Llan 8B/2, 103 1294, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Derivation of name. Latin *laevigatus*, smooth.

Diagnosis. A *Segestrespora* with a thin, folded and laevigate envelope.

Description. Pseudodyads elliptical to sub-circular in lateral view and totally enclosed within an envelope. Individual 'spores' of pseudodyad laevigate, distally convex in lateral compression, occasionally folded with walls *c*. 1 μm thick. A single darkened encircling band 1–2 μm wide joins 'spores' which are anisomorphic in *c*. 25% of observed specimens. Envelope is laevigate, < 1 μm thick, often highly folded, and varies from being closely adpressed to the dyad and difficult to resolve, to completely separated.

Dimensions. Pseudodyads 26 (29) 41 μm long, 17 (23) 31 μm wide at equator (20 specimens measured). Length to width ratio = 1·3.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. *Segestrespora membranifera* comb. nov. has reticulate ornamentation on its envelope and *S. rugosa* comb. nov. has rugulate ornamentation. One of the specimens of '*Dyadospora membranifera*' Johnson possessed a smooth envelope (pl. 7, fig. 7) and this specimen is included in this new species. Other possible records of *S. laevigata*, all from the Rhuddanian, are: Miller and Eames (1982), who stated (p. 248) that membranes were occasionally found around '*Dyadospora murusdensa*'; Strother and Traverse (1979, p. 7) who recovered 'membrane enclosed bilaterally symetrical opaque bodies'; and Richardson in Hill *et al.* (1985), who recorded 'diaphanous sheaths' (p. 29) around '*Dyadospora murusdensa*'.

Segestrespora (*Pseudodyadospora*) *rugosa* (Johnson, 1985) comb. nov.

Plate 2, figs 7–9

1985 *Pseudodyadospora rugosa* Johnson, p. 337, pl. VIII, figs 2–6.
1988 *Pseudodyadospora* sp. C, Richardson, p. 95.

Holotype and type locality. Johnson, 1985, pl. 8, fig. 5, slide TMH81-3-27, location EF M39-4, c. 175 m above the base of the Mill Hall section, Tuscarora Formation. Section – 200 m long and located 250 m above US Route 220, 1 km SE of Mill Hall, Clinton County, Pennsylvania, USA.

Figured specimens. FM 208, Pl. 2, fig. 7, slide Llan 8B/11, 077 1214; FM 209, Pl. 2, fig. 8, slide Llan 8B/6, 055 1125; FM 210, Pl. 2, fig. 9, slide Llan 8B/2, 086 1234; all sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Diagnosis. A *Segestrespora* with an envelope ornamented with regularly sinuous and closely spaced rugulae.

Description. Pseudodyads sub-circular to elliptical in lateral view, and totally enclosed within an envelope. Individual 'spores' of pseudodyad distally convex with a laevigate and occasionally folded wall *c*. 1 μm thick. A single darkened and possibly thickened encircling band, 1–2 μm wide, joins the 'spores' which are anisomorphic in *c*. 33% of the specimens. The envelope is tightly adpressed to completely separated from pseudodyad and ornamented with closely spaced, regularly sinuous, rugulae 0·5 (1) 1·5 μm wide, < 1 μm high and 0·5–1 μm apart.

Dimensions. Pseudodyads 27 (29) 31 μm long, 15 (20) 23 μm wide at equator (12 specimens measured). Length to width ratio = 1·4.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. *Pseudodyadospora* sp. C Richardson, 1988 appears identical to these spores. *Pseudodyadospora rugosa* Johnson, 1985 is similarly ornamented, but Johnson (1985, p. 337) made no mention of whether the rugulae were on an envelope or the dyad wall. However, Johnson now believes (pers. comm. 1986) that there is a closely adherent envelope surrounding her pseudodyads. The envelope surrounding *Velatitetras rugulata* sp. nov. is similarly sculptured, but encloses a cryptospore tetrad.

EXPLANATION OF PLATE 2

All figures ×1000 unless stated otherwise.

Fig. 1. *Segestrespora laevigata* gen. et sp. nov. FM 202 (slide Llan 8B/2, co-ord 103 1294; E.F. no: K59/2/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Figs 2–5. *Segestrespora membranifera* (Johnson, 1985) comb. nov. 2, FM 203 (slide Llan 8B/7, co-ord 198 1020; E.F. no: T31/3), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, ×2000. 3, FM 204 (slide 8B/7, co-ord 220 2100; E.F. no: W50/3/W49/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, ×2000. 4, FM 205 (slide Llan 8/11, co-ord 240 1170; E.F. no: Y47/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, ×2000. 5, FM 206 (slide Llan 8B/10, co-ord 130 1150; E.F. no: N45/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 6. *Segestrespora* sp.A. FM 207 (slide Llan 7B/4, co-ord 100 1015; E.F. no: K30/2), sample L1, Scrach Formation, *persculptus* Graptolite Biozone.

Figs 7–9. *Segestrespora rugosa* gen. et sp. nov. 7, FM 208 (slide Llan 8B/11, co-ord 077 1214; E.F. no: G51/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone, ×2000. 8, FM 209 (Llan 8B/6, co-ord 055 1125; E.F. no: E42/1), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 9, FM 210 (slide Llan 8B/2, co-ord 086 1234; E.F. no: H53/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 10. *Dyadospora murusattenuata* Strother and Traverse, 1979. FM 211 (slide Llan 8B/22, 138 1350; E.F. no: N65/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

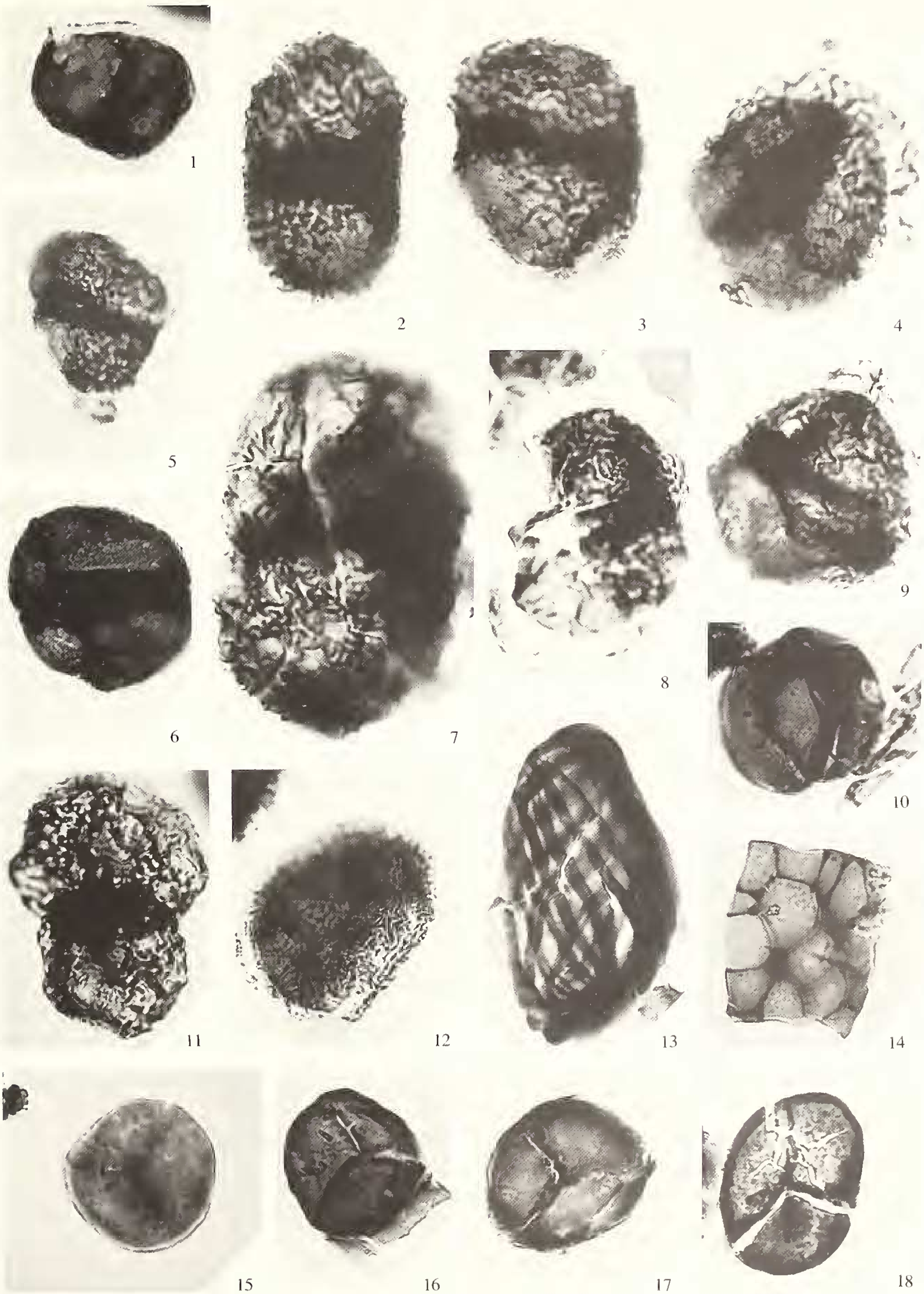
Figs 11 and 12. *Rugosphaera* cf. *R*?. *cerebra* Miller and Eames, 1982. 11, FM 212 (slide Llan 8B/8, co-ord 110 1300; E.F. no: K60/2), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 12, FM 213 (slide Llan 8B/24, co-ord 101 1080; E.F. no: K37/4), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone.

Fig. 13. *Strophomorpha ovata* Miller and Eames, 1982. FM 214 (slide Llan 3B/3, co-ord 035 1090; E.F. no: B39/1/2), sample L8, Crychan Formation, *cyphus* Graptolite Biozone.

Fig. 14. *Nematothallus* cuticle (see Edwards 1986). FM 219 (slide Llan 6/2, 237 1250; E.F. no: Y55/1), sample L21, Wormwood Formation, *sedgwickii* Graptolite Biozone.

Fig. 15. *Ambitisporites dilutus* (Hoffmeister) Richardson and Lister, 1969. FM 95 (slide Llan 6/2, co-ord 071 1160; E.F. no: G47/3), sample L21, Wormwood Formation, *sedgwickii* Graptolite Biozone.

Figs 16–18. *Ambitisporites*? *vavrdovii* Richardson, 1988. 16, FM 216 (Llan 7B/6, 090 1180; E.F. no: J48), sample L1, Scrach Formation, *persculptus* Graptolite Biozone. 17, FM 217 (slide Llan 8B/6, 138 1225; E.F. no: P53/3), sample L5, Bronydd Formation, *acinaces* Graptolite Biozone. 18, FM 218 (slide Llan 3B/1, 130 1296; E.F. no: N59/N60), sample L8, Crychan Formation, *cyphus* Graptolite Biozone.



BURGESS, Llandovery sporomorphs

Segestrespora sp. A

Plate 2, fig. 6

Figured specimen. FM 207, Pl. 2, fig. 6, slide Llan 7B/4, 100 1015, sample L1, Forestry Track F.33, Scrach Formation, *persculptus* Graptolite Biozone, latest Ordovician.

Description. Pseudodyads sub-circular to elliptical in equatorial view, and totally enclosed within an envelope. Individual 'spores' of pseudodyad distally convex, with a laevigate, occasionally folded wall *c*. 1 μm thick. A single, darkened and possibly thickened encircling band, 1–2 μm wide, joins 'spores' which are anisomorphic in *c*. 33% of the specimens. The envelope varies from closely adpressed to the pseudodyad to completely separated from it, and is ornamented with regularly distributed and closely spaced grana $< 0{\cdot}5$ μm high and wide and *c*. 0·5 μm apart.

Dimensions. Pseudodyads 29 (30·5) 35 μm long, 26 (27) 29 μm wide at equator (3 specimens only). Length to width ratio = 1·2.

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone), to early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparison. *Velatitetras* sp. A has a similarly ornamented envelope surrounding a cryptospore tetrad.

Genus DYADOSPORA Strother and Traverse, 1979

Type species. *Dyadospora murusattenuata* Strother and Traverse, 1979

(Due to the presence of naked, laevigate and permanently fused pseudodyads in the early Silurian (*Pseudodyadospora* Johnson, 1985), as well as similar enveloped forms (*Segestrespora* gen. nov.) the genus *Dyadospora* Strother and Traverse, 1979 is taken to include only non-enveloped laevigate dyads which habitually separate to produce two laevigate alete spores (see Burgess and Richardson 1991).

Dyadospora cf. *murusattenuata* Strother and Traverse, 1979

Plate 2, fig. 10

Figured specimen. FM 211, Pl. 2, fig. 10, slide Llan 8B/22, 138 1350, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Dimensions. Dyad 22 (28) 39 μm long, 20 (27) 37 μm wide at equator (5 specimens measured).

Biostratigraphic range. Early Rhuddanian (*acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. The few specimens recovered generally conform to the description of Strother and Traverse (1979), but preservation is too poor to be sure they are conspecific.

3. *Cryptospore monads*

This group encompasses monads whose wall thickness and sculpturing is comparable to that of the cryptospore tetrads and dyads but where it is more difficult to be convinced they are derived from land plants.

Genus RUGOSPHAERA Strother and Traverse, 1979

Type species. *Rugosphaera tuscarorensis* Strother and Traverse, 1979

Rugosphaera cf. *R.*? *cerebra* Miller and Eames, 1982

Plate 2, figs 11 and 12

Figured specimens. FM 212, Pl. 2, fig. 11, slide Llan 8B/8, 110 1300; FM 213, Pl. 2, fig. 12, slide Llan 8B/24, 101 1080, both sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone.

Description. Cryptospore monads sub-circular to circular in outline. In some specimens a laevigate inner body with a *c.* 1 μm thick wall can be discerned. Envelope always tightly adpressed to inner body and ornamented with closely spaced regularly sinuous to angular and rarely anastomosing rugulae 1(2)3·5 μm wide, 0·5–1 μm high and 0·5(1)1·5 μm apart.

Dimensions. Maximum diameter 23 (28) 37 μm, minimum diameter 16 (24) 30 μm (8 specimens measured).

Biostratigraphic range. Early Rhuddanian (*Acinaces* Graptolite Biozone; Text-fig. 7).

Comparisons. Rugosphaera? *cerebra* Miller and Eames is larger (38(45)55 μm in diameter), but otherwise similar. *R. tuscarorensis* Strother and Traverse has broader (1–4 μm) more widely spaced and less sinuous muri.

Genus STROPHOMORPHA Miller and Eames, 1982

Type species. Strophomorpha ovata Miller and Eames, 1982.

Strophomorpha ovata Miller and Eames, 1982

Plate 2, fig. 13

Figured specimen. FM 214, Pl. 2, fig. 13, slide Llan 3B/3, 035 1090, sample L8, Forestry Track F.33, Crychan Formation, *cyphus* Graptolite Biozone.

Description. Cryptospore monad with an elliptical to sub-rectangular outline and rounded poles. Body ornamented with low and rounded muri 0·75 (2) 3·5 μm wide separated by striae 1(2)3·5 μm across; muri are spirally arranged and converge at the poles. Wall is 1–3 μm thick and a single layer.

Dimensions. Maximum diameter 29 (46) 60 μm, minimum diameter 21 (29) 36 μm (10 specimens measured).

Biostratigraphic range. Late Rhuddanian (*cyphus* Graptolite Biozone; Text-fig. 7).

Comparisons. Strophomorpha ovata Miller and Eames is larger (48(56)65 μm) but in other ways closely comparable. *Moyeria cabottii* Cramer, 1966 is thinner-walled with narrower muri. *Qualisaspora fragilis* Richardson *et al.*, 1984 has two, much thinner, wall-layers.

Remarks. The presence of *Strophomorpha ovata* in the deeper-marine Rhuddanian aged sediments of the type Llandovery area, rather than the near-shore strata, indicates this species may be a thick-walled acritarch as opposed to a cryptospore. However, for the present it is described as a cryptospore until more evidence accumulates on its facies distribution.

Anteturma SPORITES H. Potonié, 1893
Turma TRILETES Reinsch, 1891
Subturma ZONOTRILETES Waltz, 1935 in Luber and Waltz (1938)
Infraturma CRASSITI Bharadwaj and Venkatachala, 1961

Genus AMBITISPORITES Hoffmeister, 1959

Type specimens. Ambitisporites avitus Hoffmeister, 1959

Ambitisporites dilutus (Hoffmeister) Richardson and Lister, 1969

Plate 2, fig. 15

Figured specimen. FM 95, Pl. 2, fig. 15, slide Llan 6/2, 071 1160, sample L21, Aeronian/Telychian type boundary section, Wormwood Formation, *sedgwickii* Graptolite Biozone.

Dimensions. Diameter 20 (25) 30 μm (7 specimens measured).

Biostratigraphic range. Late Aeronian (*sedgwickii* Graptolite Biozone) to early Telychian (*turriculatus* Graptolite Biozone; Text-fig. 7).

Comparisons. Ambitisporites? *vavrdovii* Richardson, 1988 has triradiate splits, not sutures, in the proximal wall and a more prominent equatorial crassitude.

Ambitisporites? *vavrdovii* Richardson, 1988

Plate 2, figs 16–18

Figured specimens. FM 216, Pl. 2, fig. 16, slide Llan 7B/6, 090 1180, sample L1, Forestry Track F.33, Scrach Formation, *persculptus* Graptolite Biozone. FM 217, Pl. 2, fig. 17, slide Llan 8B/6, 138 1225, sample L5, Forestry Track F.33, Bronydd Formation, *acinaces* Graptolite Biozone; FM 218, Pl. 2, fig. 18, slide Llan 3B/1, 130 1296, sample L8, Crychan Formation, *cyphus* Graptolite Biozone.

Description. Amb sub-triangular to triangular. Equatorial crassitude 1–3 μm wide and well defined. Proximal surface laevigate. Trilete mark distinct, is a simple split without laesurae which extends to the equator or nearly so. Distal exine 1–2 μm thick and laevigate.

Dimensions. Diameter 28 (24) 32 μm (8 specimens measured).

Biostratigraphic range. Latest Ordovician (*persculptus* Graptolite Biozone) to early Aeronian (*convolutus* Graptolite Biozone; Text-fig. 7).

Comparisons. Comparable 'trilete' spores have been described by Gray and Boucot (1971, lower Llandovery of North America), Gray *et al.* (1982), ?Caradoc of Libya), Johnson (1985, lower Llandovery of North America), and Richardson (1988, late Ordovician and early Llandovery of Libya). Moreover, Gray *et al.* (1982) have shown that closely comparable spores can be derived from mechanically fragmented tetrads of the genus *Tetrahedraletes*. *Ambitisporites avitus* Hoffmeister has its earliest records in the later Llandovery of North Africa and has more prominent trilete marks with sutures and laesurae, never a simple split.

COMPARISON WITH SIMILARLY AGED MICROFLORAS WORLDWIDE

Several continents have been recognized in the Silurian (Livermore *et al.*, 1985). These include Laurentia (North America and Europe north of the Iapetus suture), Baltica (Europe and Russia south of the Iapetus suture and north of the Hercynian suture), and Gondwana (Africa, South America and Australasia). Uppermost Ordovician and Llandovery spore microfloras from the type Llandovery area are compared with those from these continents.

Late Ordovician and early Silurian assemblages

Baltica. Vavrdova (1982, 1984, 1988) has described a diverse assemblage of cryptospore tetrads from the late Ordovician (*bohemicus* graptolite Biozone) Kosov Formation in Czechoslovakia. Many specimens appear similar, both in size, and sculptural patterning on their envelopes, to those from the type Llandovery area. For example, tetrad types A, B and C of Vavrdova (1984) are similar to *Tetrahedraletes medinensis* var. *parvus*, *Velatitetras reticulata* and *Velatitetras* sp.A respectively. 'Trilete spores' (*Ambitisporites*? *vavrdovii*) were also recorded in Czechoslovakia.

Laurentia. Sporomorph assemblages from the late Ordovician and early Llandovery of North America are also similar to those from the type Llandovery area in that they are predominantly composed of cryptospores (Gray and Boucot 1971; Cramer and Diez 1972; Strother and Traverse 1979; Miller and Eames 1982; Gray 1985; Johnson 1985; Gray 1988). In many of these studies (Strother and Traverse 1979; Miller and Eames 1982; Johnson 1985) the North American cryptospore tetrads are considerably larger ($\bar{x}$ = *c*. 50 μm) than those from the type Llandovery area ($\bar{x} = 26$ μm). However, those cryptospore tetrads obtained from upper Ordovician and basal Llandovery strata by Gray (1985, 1988) are of similar size ($\bar{x} = < 30$ μm) and some possessed highly comparable envelopes.

Ambitisporites? *vavrdovii* has also been recorded from the Llandovery of North America (Gray and Boucot 1971; Gray 1985).

Gondwana. A diverse assemblage of cryptospores has been recently described from subsurface material of late Ordovician to late Llandovery age in north-east Libya (Richardson 1988). This assemblage comprises around ten species of cryptospore tetrad, eleven species of pseudodyad, two species of true dyad, three species of cryptospore monad and three species of trilete miospore. Some of these are identical to those from the type Llandovery area, although eleven of the species discovered in Libya have not been seen in Britain.

Other late Ordovician and early Llandovery records of sporomorphs (all *Tetrahedraletes*) from Gondwana are from the Soom Shale Member of the Cedarberg Formation, Table Mountain Group, South Africa (Gray *et al.* 1986); and from the Vila Maria Formation of the Parana Basin, Brasil (Gray *et al.* 1985). Furthermore, specimens of *Tetrahedraletes* recovered by Gray *et al.* (1982) from the ?Caradoc strata of the Murzurk Basin in Libya are closely comparable to uppermost Ordovician and lower Llandovery specimens from the type Llandovery area.

Late Llandovery assemblages

Late Llandovery sporomorph assemblages are known from Baltica, Laurentia and Gondwana (Hoffmeister 1959; Cramer 1968, 1969; Smith 1975; Emo and Smith 1978; Aldridge *et al.* 1979; Pratt *et al.* 1978; Smith 1979, 1981; Gray 1985; Hill *et al.* 1985; Gray 1988; Richardson 1988). All these investigations have demonstrated low spore diversity during this period with smooth-walled trilete miospores of the genus *Ambitisporites* predominating. This is comparable with the late Llandovery spore assemblage obtained from the type Llandovery area.

PALYNOFACIES

Preliminary investigation of the palynofacies in the type Llandovery area (Burgess 1987), has demonstrated large numbers of cryptospores and reworked acritarchs (Tremadoc and Ordovician) in the Scrach Formation and lower Bronydd Formation. This indicates deposition in nearshore palaeoenvironments, as previously suggested following mega fossil and sedimentological investigations (Cocks *et al.* 1984). Higher in the Bronydd Formation and throughout the Crychan, Trefawr, Rhydings, Wormwood, and Cerig Formations an extremely sparse microflora with few spores was obtained. The palynological assemblage, macro-fauna and sedimentology (Cocks *et al.* 1984) of these formations indicate deposition in off-shore shelf conditions at a considerable distance from land. It is thus probable that the sporomorph assemblage obtained from the base of the Llandovery type section is more representative of its age than that from the late Rhuddanian through to the early Telychian (later Telychian not sampled).

BIOSTRATIGRAPHY

Text-figure 7 presents the stratigraphical ranges of the sporomorphs recovered from the type Llandovery area. The two fold sub-division of the sequence is closely comparable to that recognized by Gray (1985, 1988), Richardson and McGregor (1986) and Richardson (1988).

Gray (1985) first noted the presence of a cryptospore-dominated spore assemblage in the Late Ordovician and Early Silurian and named this 'Microfossil Assemblage Zone 1'. It has recently been formally named the *Nodospora* sp. A (= *Velatitetras laevigata*) – *Dyadospora murusdensa* Assemblage Biozone (Richardson 1988), and has been further subdivided into three Assemblage Biosubzones. Samples L1–L20, from the late *persculptus* to late *sedgwickii* Graptolite Biozones of the type Llandovery area, fall within the *Dyadospora membranifera* (= *Segestrespora membranifera*) – *Pseudodyadospora* sp. B Biosubzone of Richardson (1988). *Ambitisporites*? *vavrdovii* is present in this Biosubzone, but as these spores probably derive from mechanically fragmented cryptospore tetrads (Gray *et al.* 1982) they do not represent the earliest records of trilete miospores.

Gray (1985) also recognized a later Llandovery spore zone typified by smooth-walled trilete miospores and named it 'Microfossil Assemblage Zone 2'. This had been named the *Ambitisporites avitus* assemblage by Richardson (1974) and was later termed the *Ambitisporites dilutus* – *A. avitus* Assemblage Zone by Richardson and McGregor (1986). In the type Llandovery area this zone is recorded from samples L21–L23 (late Aeronian *sedgwickii* Graptolite Biozone to early Telychian *turriculatus* Graptolite Biozone).

The oldest specimens of *Ambitisporites dilutus* recorded from the late Aeronian (*sedgwickii* Graptolite Biozone) Wormwood Formation are the oldest known with precise dating. Their recovery enables the reference section for the base of the *Ambitisporites avitus* – *A. dilutus* spore Assemblage Zone of Richardson and McGregor (1986) to be defined as sample L21 (= locality 162 of Cocks *et al.* 1984) in the Type Aeronian/Telychian Boundary Section of the type Llandovery area.

A review of the literature suggests that the appearance of true *Ambitisporites* (not *Ambitisporites*? *vavrdovii*) occurs at comparable horizons globally. For instance, elsewhere in the British Isles *Ambitisporites* first occurs in the Aeronian *Pentamerus* Beds of the Welsh Borderland (Aldridge *et al.* 1979), and the Telychian *griestonensis* Graptolite Biozone of Ireland (Emo and Smith 1978; Smith 1981). Furthermore, in North America the incoming of *Ambitisporites* is placed at around the C2–C3 boundary (Gray 1985; 1988) which is equivalent to slightly lower in the Aeronian *sedgwickii* Graptolite Biozone than recorded in the type area. In North Africa *Ambitisporites* is also first recorded in the Aeronian (Hoffmeister 1959; Hill *et al.* 1985; Richardson and McGregor 1986; Richardson 1988).

PALAEOBOTANICAL IMPORTANCE

That cryptospores may provide evidence of pioneering land plants has been much debated (Gray and Boucot 1971, 1977; Gray 1985, 1988; Taylor, 1982). However, as they have yet to be recovered from the sporangia of a land-plant megafossil their derivation from this source remains unproven. The best evidence for a land plant source comes from their abundant recovery in fluviatile sediments of North America (Johnson 1985; Strother and Traverse 1979), and their similarity to spores produced by certain extant hepatics (Gray 1985).

Trilete miospores, on the other hand, have been recovered from within the sporangia of the rhyniophytoid land plant *Cooksonia pertoni* in the late Silurian (Lang 1937; Fanning *et al.* 1988). Consequently, the Llandovery examples may be derived from a similar source and those from the late Aeronian may provide the oldest evidence of such organisms.

In this study the oldest cuticles probably derived from land plants (Edwards 1986) were recovered from the late Aeronian (Pl. 2, fig. 14). They are apparently absent in the Rhuddanian, even though these samples were the most nearshore investigated and sporomorphs were at their most abundant and diverse. Other studies have reported cuticles in the middle Caradoc and later Ordovician (Gray *et al.* 1982; Gray 1985; Vavrdova 1988). Internally thickened tubes (Burgess and Edwards in press) were also not recorded from the type Llandovery area, even though Pratt *et al.* (1978) and Gray (1985) found them in upper Llandovery sediments of the USA, and they are present in basal Wenlock strata of the type Wenlock area (Burgess and Richardson 1991). Their absence may be related to the fact that extremely distal sediments were sampled in the late Llandovery of the type area. However, the facies in the early Rhuddanian are regarded as suitable for their recovery and their absence at this level may be genuine.

In conclusion, this study provides some evidence to support the assertions of Gray (1985) and Edwards and Burgess (1990), that a major change in the land-flora occurred in the late Aeronian. This change was from a flora dominated by cryptospore-producing plants, to a flora dominated by trilete miospore-producing plants. Moreover, this change appears to have occurred at approximately the same stratigraphical horizon worldwide.

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